Stereoscopic vision: **What's the first step?**

Benjamin T. Backus

Neurons in primary visual cortex respond to binocular disparity, the raw material of stereoscopic depth perception. Although these neurons are probably essential to depth perception, a recent study has shown that they are unable to compute depth itself.

Address: Department of Psychology, University of Pennsylvania, 3815 Walnut Street, Philadelphia, Philadelphia 19104-6196, USA.
E-mail: backus@psych.upenn.edu

Current Biology 2000, 10:R701–R703

0960-9822/00/$ – see front matter

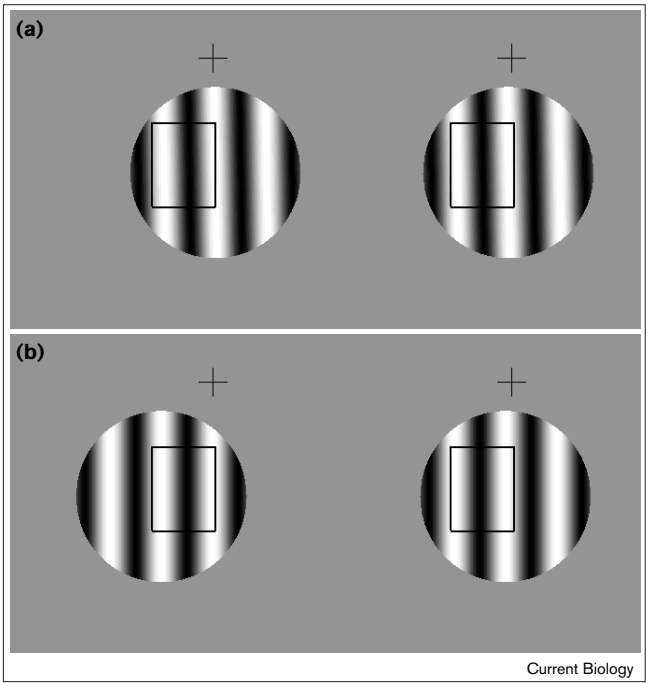
The left and right eyes get slightly different views of the world, and the resulting binocular disparities allow the visual system to construct vivid percepts of depth. The neural basis for most of this process is still completely mysterious. The exception is the front end — the first stages of disparity processing that occur in what is variously called primary visual cortex, striate cortex or area V1. Cumming and Parker [1] have now made electrophysiological recordings in area V1 of the macaque monkey that clarify the role of these neurons. Contrary to recent suspicions, the V1 neurons do not encode depth. Instead, they are limited to extracting so-called 'absolute' retinal disparities within small patches of the visual field. Thus, other cortical areas are needed to create the percept of depth.

The visual system uses disparity in two ways. One is to control the convergence of the eyes. For this, the visual system must calculate absolute retinal disparity, which is the displacement of an image, or piece of an image, on one retina relative to its location on the other retina. When you fixate an object, its images fall on your foveas with zero disparity. The second, more complicated use of disparity is to determine the depths of objects in a scene. This can be done using relative disparity, which is the difference in absolute disparity between two spatially separated parts of the binocular fused image. Fluctuation in the eyes' convergence causes fluctuation in absolute disparity but not relative disparity, which could explain why relative depth judgments are very precise [2,3]. Last year, Cumming and Parker [4] showed that V1 neurons in the macaque do not encode relative disparity. But it remained possible that neural firing rates would reflect depth *per se*, perhaps as the result of feedback from higher cortical areas.

Last year's finding [4] agreed with a well validated model of disparity-selective cells in the anaesthetized cat [5–7]. In this model, a 'simple' cell monitors corresponding patches of retina in the left and right eyes. The cell responds when both retinal patches receive their optimal inputs, which for each retina is a sinusoidal image component — a grating of light and dark stripes — at a particular phase relative to the patch. A 'complex' cell combines the outputs from a select group of simple cells, such that it responds to a particular interocular phase difference, without regard to the exact positions of the images on the retinae. The important point here is that, in this model, simple and complex cells both encode a form of absolute retinal disparity.

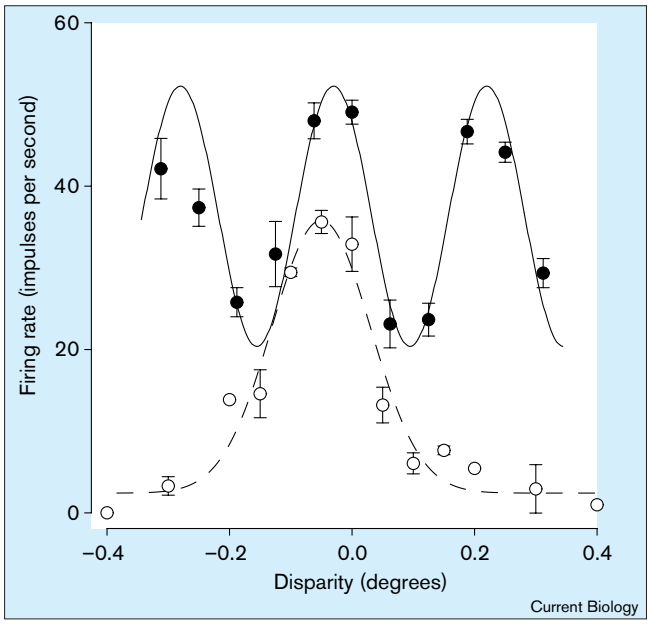
But does this model accurately describe V1 cells in alert primates? Primates might differ from cats, and the depth percepts in alert animals might exert top-down influences on the cells in V1. Area V1 gets input from other cortical areas, and the activity of V1 neurons can be modulated by attention and by stimuli that fall outside of their small, classical receptive fields. Cumming and Parker [1] tested explicitly whether perceived depth can influence neuronal responses in V1. To do this, they exploited a curious property of stereoscopic vision [8]: the multiple possible depth interpretations that are possible with periodic binocular stimuli.

Figure 1



The stimulus of Cumming and Parker [1], for free fusion viewing. The rectangles diagram the receptive field of a binocular neuron. In **(a)** and **(b)**, the local pattern that impinges on the receptive field is the same, but the perceived depth of the patch, which depends on the global disparity of the patches as wholes, is different in the two cases.

Figure 2



The response of a neuron to patterned patches, as a function of patch disparity. Solid dots plot responses for patches that contained a vertical grating. The spatial period of the grating was 0.25°. The data are fitted with a sinusoid. Open dots plot responses for random-dot stimulus patches. They are fitted with a Gabor function.

If a horizontally repeating pattern is shown to both eyes, then there are many ways the brain could match up the left and right images, yielding many different perceived depths for the pattern. With the stimulus shown in Figure 1, for example, any black stripe in one image could be matched up with any black stripe in the other. In general, the depth one sees results from the match that is closest to an absolute disparity of zero. In Figure 1a, for example, the second dark bar in the left image and the second dark bar in the right image have nearly the same positions relative to their respective fixation marks (the crosses). These bars will therefore be matched, and the depth of the bar will be similar to the depth of the fixation marker. But a different match can be forced by using bounded stimuli, as in Figure 1b. The pattern as a whole has non-zero disparity, yet the second bars in the left and right images are once again matched to each other — even though a match to the third bar in the right image would have lower disparity.

In panels (a) and (b) of Figure 1, the portion of the patch that falls within the rectangle is the same. A neuron that has the rectangle as its receptive field, and no feedback based on perceived depth, will not see anything different between (a) and (b). But if depth does affect the neuron, then it will respond differently in the two situations, because the perceived depths are different. The procedure of Cumming and Parker [1] was to find a disparity-selective neuron in V1, map its classical receptive field using a small flashing bar, and then show stimuli like those in Figure 1 to the monkey.

The monkeys (two of them) were trained in advance to make special eye movements to indicate whether a patch was closer or farther than fixation. These eye movements were monitored with scleral search coils (not simultaneous with the electrophysiology). Like humans, the monkeys indicated that the stimulus had the perceived depth that was specified by the target as a whole. But even though the monkey's behavioral response went from 'far' to 'near' over the range of disparities tested, the activity of the typical neuron was quite different: it showed separate peaks in activity, at patch disparities that were multiples of the grating period. In other words, the stimuli in panels (a) and (b) of Figure 1 were indistinguishable to a neuron that had a receptive field at the location of the rectangles.

Data for a typical neuron are shown by the filled circles in Figure 2. This neuron shows peak activity at not one, but three different disparities, corresponding to multiples of the grating period. Of 129 tests in 117 neurons, 81 were strongly periodic, showing large secondary peaks at disparities that were multiples of the grating period — that is, secondary peaks with amplitudes that were 80% or more of the largest peak's amplitude. Only a few disparity-tuned neurons were actually aperiodic. This was in fact to be expected for any neuron whose receptive field was not mapped very accurately by the flashing bar technique, as a large disparity would then place the stimulus outside of the receptive field. But an alternative explanation is that the neuron was tuned to a single perceived depth, as perceived depth is what varied monotonically with disparity in the stimulus.

This concern, that neurons might be tuned to global depth rather than local absolute disparity, was addressed by repeating the experiments with random dot stereogram patches. Because V1 neurons are broadly tuned for spatial frequency — they respond over a range of grating periods — a random dot stereogram, which contains many spatial frequencies, excites a neuron best at the neuron's preferred disparity. For most of the periodic neurons, the random dot stimulus was maximally effective at one of the disparities where the grating stimulus also evoked maximal firing (an example is shown in Figure 2). But for the aperiodic neurons, there was little relationship between the maximally effective disparities of the two types of stimulus. We can reasonably conclude, therefore, that the aperiodic neurons were not signaling the perceived depth of the stimulus.

Our understanding of stereoscopic vision is improving. Areas of current research include the organization of disparity-selective neurons in topographic maps, the contributions

of other visual areas besides V1 to stereoscopic tasks, and how stereoscopic information is combined with motion, occlusion and other cues to depth. Binocular stimulation experiments, like those that characterized disparity-selective neurons in the cat [7], are being done in the macaque (see [9], for example). The biasing of perceptual responses through direct stimulation of area MT was reported last year ([10]; see [11] for a recent review of many of these findings). Although we still have very little idea how percepts are represented in the brain, we can now relate some aspects of depth perception to the known properties of neurons — and we know that V1 neurons provide only the first steps in what could be a rather complicated process.

Acknowledgements
Thanks to Ted Abel and Marc Schmidt for their very helpful comments on the text.

References

1. Cumming BG, Parker AJ: **Local disparity not perceived depth is signaled by binocular neurons in cortical area V1 of the Macaque.** *J Neurosci* 2000, **20:**4758-4767.
2. Westheimer G: **Cooperative neural processes involved in stereoscopic acuity.** *Exp Brain Res* 1979, **36:**585-597.
3. Prince SJ, Pointon AD, Cumming BG, Parker AJ: **The precision of single neuron responses in cortical area V1 during stereoscopic depth judgments.** *J Neurosci* 2000, **20:**3387-3400.
4. Cumming BG, Parker AJ: **Binocular neurons in V1 of awake monkeys are selective for absolute, not relative, disparity.** *J Neurosci* 1999, **19:**5602-5618.
5. Freeman RD, Ohzawa I: **On the neurophysiological organization of binocular vision.** *Vision Res* 1990, **30:**1661-1676.
6. Ohzawa I, DeAngelis GC, Freeman RD: **Encoding of binocular disparity by complex cells in the cat's visual cortex.** *J Neurophysiol* 1997, **77:**2879-2909.
7. Anzai A, Ohzawa I, Freeman RD: **Neural mechanisms for encoding binocular disparity: receptive field position versus phase.** *J Neurophysiol* 1999, **82:**874-890.
8. McKee SP, Mitchison GJ: **The role of retinal correspondence in stereoscopic matching.** *Vision Res* 1988, **28:**1001-1012.
9. Livingstone MS, Tsao DY: **Receptive fields of disparity-selective neurons in macaque striate cortex.** [published erratum appears in *Nat Neurosci* 2000, **3:**409]. *Nat Neurosci* 1999, **2:**825-832.
10. DeAngelis GC, Newsome WT: **Organization of disparity-selective neurons in macaque area MT.** *J Neurosci* 1999, **19:**1398-1415.
11. DeAngelis GC: **Seeing in three dimensions: the neurophysiology of stereopsis.** *Trends Cogn Sci* 2000, **4:**80-90.